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Review Article

The role of microbiomes in animal invasions: a scoping review

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Abstract

Despite increasing evidence for the contribution of microbiomes to host fitness and evolution, their role in the adaptation and successful establishment of invasive animal species remains underexplored. Animal microbiomes can mediate key host phenotypic traits such as energy metabolism, detoxification and disease resistance. Therefore, harbouring a highly functional microbiome may be advantageous in the context of invasion, where small host populations must rapidly adapt to new environmental conditions. We conducted a scoping review of studies focusing on microbiomes and animal invasions to explore the extent and nature of research efforts on this topic and to identify general patterns that may help elucidate the relationship between host microbial communities and invasiveness. The analysis of 147 articles published between 2006 and 2024 showed a steady increase in the research output on the topic, in parallel with growing interest in biological invasions and technical and theoretical advances in microbiome research. However, the application of new analytical approaches that go beyond taxonomic characterisation remains limited and the research output is still heavily biased towards invasive invertebrates. Although most of the reviewed research was descriptive, a more detailed assessment of a subset of 43 studies using a comparative design revealed some recurring patterns. Host microbiomes in the introduction range tend to diverge from those in the native range, but invasive populations generally retain a core of microorganisms involved in key phenotypic traits such as disease resistance. Studies that have examined the microbiomes of invasive species along their invasion pathway highlight how stochastic events, propagule pressure and population mixing are relevant drivers of microbial community assembly during introductions. Comparisons of the microbiomes of invasive species and co-occurring, outcompeted native species often suggest that some of the observed phenotypic differences driving their interactions are microbiome-mediated. However, to date, only a handful of studies have been able to establish the mechanistic link between microbiomes and host invasiveness using an experimental design. While observational studies remain valuable at this early stage, we advocate for a wider use of novel technologies and experimental approaches to generate robust functional and mechanistic information that will strengthen their inferential value. As more system-specific studies become available, meta-analytical approaches may allow us to uncover broader eco-evolutionary patterns and ultimately elucidate the role of microbiomes in animal invasions.

Key words: Adaptation, alien species, biological invasions, invasiveness, invasive species, metagenomics, microbial community, microbiota

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Introduction

Most animals harbour complex communities of microorganisms, the animal-associated microbiota (Berg et al. 2020) residing in and on their bodies. The microbiota of a single host can include hundreds of different taxa belonging to Bacteria, Archaea, other eukaryotes and viruses. Some of these microorganisms benefit from a relatively stable and protected environment while providing their hosts with functions and services that are often crucial to their fitness (Moran et al. 2019), such as fermentative digestion in ruminants (Mackie 2002; Moraïs and Mizrahi 2019) or skin toxicity in newts (Vaelli et al. 2020).

Over fifteen years ago, Zilber-Rosenberg and Rosenberg (2008) proposed the hologenome theory of evolution, arguing that all eukaryotes should be seen as one with their microbiomes (i.e. the living microbiota plus all of its structural and genetic elements, products and metabolites, Berg et al. (2020)), as they represent a single evolutionary unit (the holobiont) upon which natural selection acts. The need and appropriateness for such a profound shift in paradigm are still debated (Douglas and Werren 2016; Madhusoodanan 2019), but it is generally undisputed that hosts and their microbiota influence each other's ecology and evolutionary trajectories (Koskella and Bergelson 2020; Moeller and Sanders 2020).

In the last decades, evidence for a role of the microbiome in animal fitness, adaptation and evolution has been increasing (Moeller and Sanders 2020), mostly thanks to advances in sequencing technologies that allow for a more in-depth study of complex microbial communities (Larsen and Matocq 2019; Berg et al. 2020). The microbiome appears to be intertwined with a wide range of host traits spanning from nutrition (Dearing and Kohl 2017) to reproduction (Comizzoli et al. 2021), behaviour (Johnson and Foster 2018; Davidson et al. 2020), energy metabolism and thermoregulation (Nicholson et al. 2012; Fontaine and Kohl 2023), immunity and resistance to infections (Gerardo et al. 2020; McLaren and Callahan 2020). Moreover, the microbiota has been hypothesised to increase host resilience to environmental challenges and serve as a mechanism for rapid adaptation, owing to its ability to undergo genomic changes at a much faster rate than animal genomes over short periods of time (Alberdi et al. 2016; Kolodny and Schulenburg 2020; Suzuki and Ley 2020). However, our current knowledge of specific mechanisms and processes linking the microbiome with host adaptation is still largely based on humans and laboratory animals, while mechanistic studies on wild populations are scarce, mostly due to limitations in experimental and analytical approaches (Martin Bideguren et al. 2024).

Biological invasions occur when a — usually small — number of individuals are translocated by humans to a new area outside their natural range, where they establish a viable population and spread away from the point of introduction (Blackburn et al. 2011). Invasions are, therefore, a dynamic process that involves several stages, during which invaders will face multiple biotic and abiotic challenges (Catford et al. 2009; Daly et al. 2023). The severity of these challenges depends on the novelty of the invaded environment and the eco-evolutionary experience of the invading species (Saul et al. 2013; Saul and Jeschke 2015). When the conditions in the new range differ substantially from those in the native range, rapid adaptation may be required for the invasion to be successful (Suarez and Tsutsui 2008; Erfmeier 2013). It stands to reason then that the microbiome, by affecting several key host phenotypic traits, could mediate alien species' adaptation and invasiveness at any of the invasion stages. For instance, having a highly plastic and/or diverse microbial community at

introduction could facilitate rapid adaptation to the new environmental conditions and ensure introduced hosts' survival and successful establishment (Alberdi et al. 2016; Kolodny and Schulenburg 2020). At the same time, it is possible that, in some circumstances, it may be advantageous for some alien species to have a highly efficient and specialised native microbiota that is conversely resistant to change. Later on, the microbiome could modulate reproductive traits or disease resistance, promoting proliferation and spread, while possibly giving invaders a competitive advantage over native competitors (McLaren and Callahan 2020; Comizzoli et al. 2021).

However, as yet, the link between microbiomes and animal invasions remains somewhat underexplored. It is important to note that the interaction between microbiomes and invasions is likely to go both ways and disentangling causality can be challenging. As illustrated in Fig. 1 and mentioned above, microbiomes are indeed likely to affect the invasion process by influencing the invasiveness of introduced species, but, at the same time, the invasion process is likely to affect the microbiomes of both invasive hosts and native ecosystems (both the biotic and abiotic components).

For instance, some animal species — especially aquatic or soil invertebrates — have the capability to alter the environmental microbiota surrounding them via microbiome excretion and/or their mechanical or chemical actions. This can increase habitat invasibility and greatly affect local communities, facilitating the establishment and spread of invaders (Malacrinò et al. 2020). This latter mechanism has received considerable attention in plant invasions, where the interaction between soil and rhizosphere microbiomes and invasive plants has long been studied (e.g. Inderjit and van der Putten (2010); Coats and Rumpho (2014); Traveset and Richardson (2014)) and often explored within the framework of the invasional meltdown hypothesis (Simberloff 2006; Zhang et al. 2020). Similarly, the alteration of environmental microbiomes by invasive soil invertebrates has been addressed quite extensively (e.g. Paudel et al. (2016); Ferlian et al. (2018)), while, when considering the host-associated

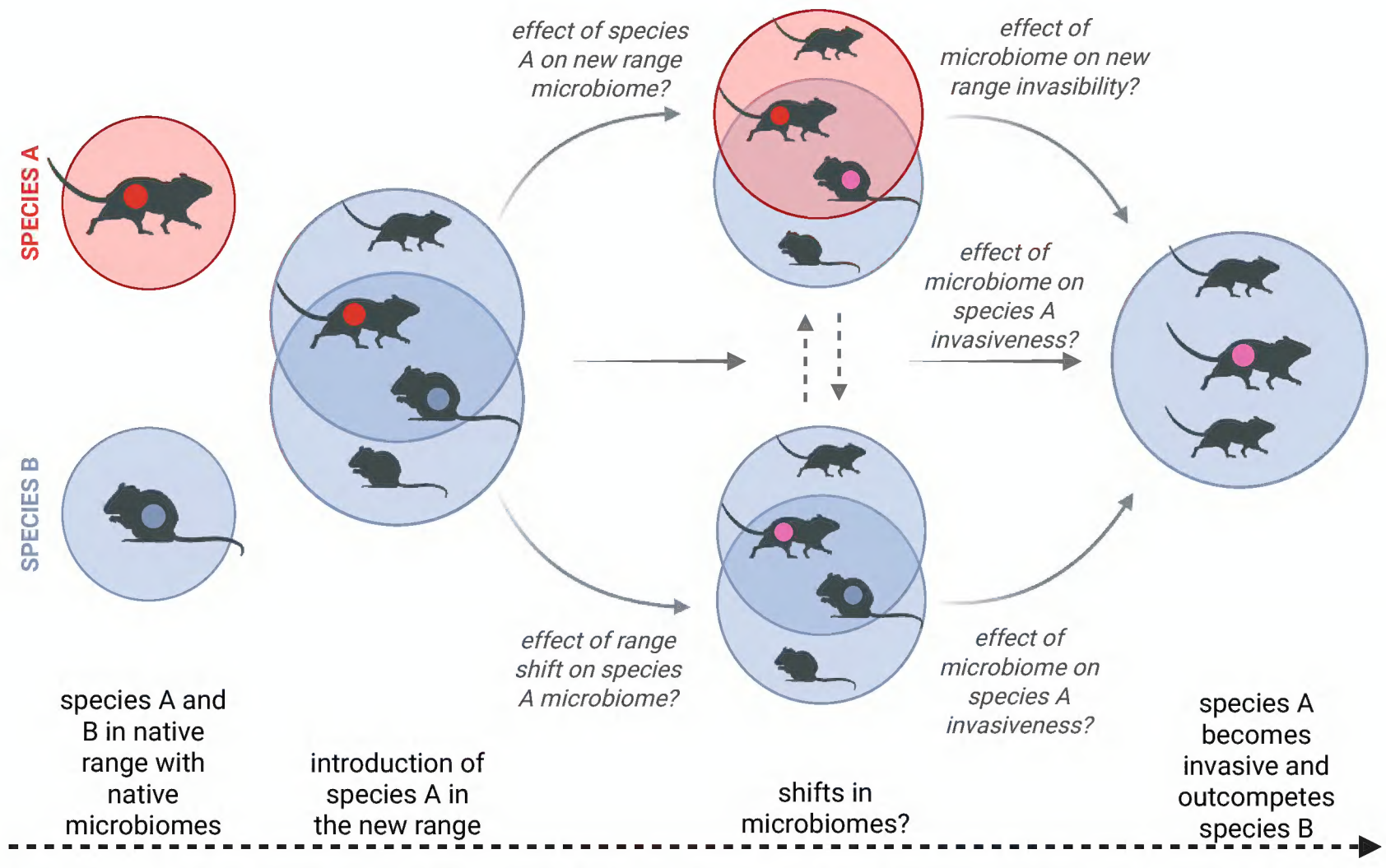

SPECIES A
SPECIES B
effect of species A on new range microbiome?
effect of microbiome on new range invasibility?
effect of microbiome on species A invasiveness?
effect of range shift on species A microbiome?
effect of microbiome on species A invasiveness?
species A and B in native range with native microbiomes
introduction of species A in the new range
shifts in microbiomes?
species A becomes invasive and outcompetes species B

Figure 1. Microbiome dynamics during invasions. Illustration of the potential two-way interactions between animal microbiomes and the invasion process. Created in BioRender (https://BioRender.com/d20m325).

microbial community and how it might facilitate animal invasions, the literature is more sparse. An exception may be insects, a taxon for which several host-microbial symbiotic interactions have been well characterised (Frago et al. 2012; Brinker et al. 2019). Indeed, almost a decade ago, Lu et al. (2016) proposed a conceptual framework of mechanisms by which symbiotic microbes may influence insect invasions.

To collate up-to-date evidence on this topic, extend the analysis to vertebrates and highlight current knowledge gaps and research perspectives, we conducted a scoping review (Arksey and O'Malley 2005; Levac et al. 2010; Peters et al. 2020) of studies dealing with animal invasions and the microbiota. The analysis of 147 articles published between 2006 and 2024, filtered from a pool of 1240 screened publications, enabled us to first explore the extent and nature of the research effort on the topic. Then, we identified general patterns from a subset of 43 studies that focussed specifically on host-associated microbiomes and that, by virtue of their comparative design, may contribute to our understanding of the potential role of animal microbiomes in invasiveness.

Literature search and analysis

The literature search was conducted in May 2024 using both Web of Science and Scopus platforms and following the PRISMA protocol (Page et al. 2021). We searched for the following terms in titles, abstracts and keywords: ("invasive species" OR "alien species" OR "invasive alien species" OR "IAS" OR "invasiveness" OR "non-native") AND ("microbiome" OR "microbiota" OR "microbial communit*" OR "metagenom*" OR "bacterial communit*"). Articles were not limited based on their year of publication, but were only included if they were published in peer-reviewed journals and written in English. The obtained list of articles was first deduplicated, removing 579 records. We then screened the titles and abstracts of the resulting 1240 articles, based on the following set of inclusion criteria:

1. the study included at least one invasive animal as a focal species (hence, studies not pertaining to invasion biology or focussing on plant or bacterial invasions were excluded); and
2. the study investigated the focal species' microbiota and/or the impact of the focal species on the microbiota of either a native counterpart or the local environment; and
3. the study examined the microbiota from a community ecology perspective. Hence, studies that only focussed on the pathobiome or on specific bacteria as a means for biocontrol were excluded.

Concerning the first criterion, although the term "invasive" was sometimes used more loosely in the retrieved studies, we included only studies where the translocation of the focal species to a new geographic range was human-mediated, either intentionally or unintentionally.

Deduplication and title and abstract screening were conducted using Rayyan (Ouzzani et al. 2016). A total of 1076 articles were removed during the title and abstract screening, resulting in 164 articles eligible for the next, full-text, screening. During this second screening, another 17 articles were excluded for not fitting the inclusion criteria listed above. A resulting 147 publications were included in the review. The PRISMA flowchart and the final set of articles are included as Suppl. materials 1, 2, respectively.

Table 1. List of descriptors used to classify the 147 articles included in the present review. A detailed explanation of the study design descriptors can be found in Suppl. material 3.

Article type	Animal group	Animal taxon	Target species	Geographic design	Study design	Microbiota location	Method
Research	Invertebrate	Arthropod	Only invasive sp.	Only native range	Comparative: range and host	Only environment	Amplicon-based sequencing
Review	Vertebrate	Invertebrate (Other)	Only native sp.	Only introduction range	Comparative: range	Gut	Shotgun metagenomics
		Amphibian	Comparative	Only invasion wave	Comparative: host species	Multiple organs/ tissues	Other
		Bird		Comparative	Comparative: IAS[a] traits	Oral	
		Fish			Descriptive: IAS[a]	Skin/Exoskeleton	
		Mammal			Descriptive: impact	Whole specimen	
		Reptile					

[a]Invasive Alien species.

The analysis of included literature was conducted in two stages. First, each of the 147 articles was classified using the descriptors listed in Table 1. Temporal publication trends were explored in terms of target host taxon, study design and methodology for microbiome characterisation. Summary statistics and data visualisation were done using R statistical software (v4.4.1, R Core Team 2023).

Second, we selected the subset of studies that focussed specifically on host-associated microbiomes and used a comparative design to address the hypothesis of a microbial contribution to invasiveness. This led to the identification of 43 articles either comparing: i) the microbiota of an invasive versus a native species, ii) the microbiota of an invasive species in the introduction versus the native range or iii) the microbiota of an invasive species along the invasion wave. From this subset of selected papers, we identified the main recurring patterns and will report a qualitative synthesis of their key findings.

Trends in animal invasions and microbiome research

The 147 papers which met all the inclusion criteria spanned 2006-May 2024, with a median publication year of 2020, demonstrating a steady increase in output over time (Fig. 2a). This increase happened in parallel with the growing interest in biological invasions and with technical and theoretical advances in microbiome research. Original research composed 95.2% (n = 140) of the included papers, while the remaining 4.8% (n = 7) were review articles. Three of the reviews addressed the impact of invasive earthworms on local soil microbiota (McLean et al. 2006; Paudel et al. 2016; Ferlian et al. 2018), three were specific to some invasive insect taxa (*Aedes albopictus*: Garrido et al. (2023); *Spodoptera frugiperda*: Kenis et al. (2023); Tephritidae fruit flies: Hafsi and Delatte (2023)) and the last one is the aforementioned review by Lu et al. (2016) on the role of symbionts in insect invasions.

The classification of the 140 research articles by the methodology used to characterise the microbiota yielded that the vast majority (87.9%, n = 123) of papers applied a targeted amplicon sequencing-based approach (16S rRNA for prokaryotes, 18S rRNA for eukaryotes, ITS for fungi or a combination of these).

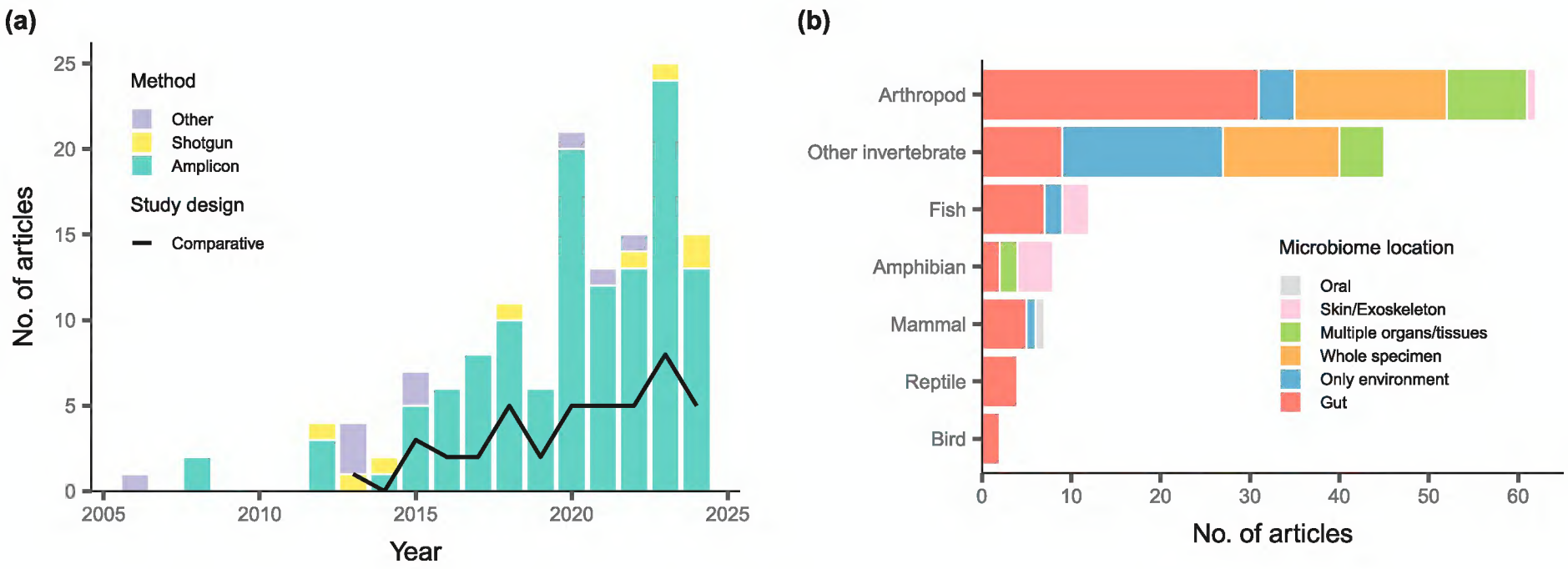


Figure 2. Trends in microbiomes-animal invasions research. Trends in the research output on microbiomes and animal invasions **a** number of articles published by year, methods used to characterise the microbial community and study design (the black line indicates the number of comparative studies); and **b** number of articles published by invasive host taxon and location of the target microbial community.

The remaining 12.1% used shotgun metagenomics (5.7%, n = 8), while the rest relied on other approaches (6.4%, n = 9), such as Restriction Fragment Length Polymorphisms (RFLP), microscopy or staining (Fig. 2a). Amplicon sequencing (or marker-gene analysis) is a well-tested, fast and relatively cheap method to characterise microbial communities from a taxonomic point of view (Knight et al. 2018; Pérez-Cobas et al. 2020). However, it fails to capture functional information that is crucial to link the microbiota structure and composition to host traits (Knight et al. 2018). While indirect functional inference techniques such as PICRUst or Piphilinn (Langille et al. 2013; Iwai et al. 2016) exist, the limited representation and biases of bacterial genome databases challenge the accuracy of indirect functional inferences in wild animals (Pérez-Cobas et al. 2020; Leonard et al. 2025). Shotgun metagenomics on the other hand, by sequencing a broad non-targeted representation of the genetic material present in a sample, enables a direct functional characterisation of the microbiota (Knight et al. 2018; Pérez-Cobas et al. 2020). In particular, genome-resolved metagenomics allows us to assemble the genomes and perform functional annotation even of previously undescribed taxa (Quince et al. 2017), which often represent the bulk of wild animals' microbiomes (Levin et al. 2021; Leonard et al. 2025). However, shotgun metagenomics remains a more costly, time-consuming and data heavy approach, which might explain why its application to invasion biology-microbiome studies is still limited.

Most research articles focused on invasive arthropods (44.3%, n = 62) or other invertebrates (32.1%, n = 44), whereas vertebrates were the focus of 23.6% (n = 33) of the articles (Fig. 2b). Most vertebrate studies regarded fish (n = 12), amphibians (n = 8) or mammals (n = 7), with only a handful of studies on the microbiota of invasive reptiles (n = 4) or birds (n = 2). This strong taxonomic bias in favour of invertebrates is probably due to multiple reasons. Invertebrates and, especially, arthropods, represent the vast majority of animal invasions worldwide (Pyšek et al. 2020; Seebens et al. 2021) and are amongst those with the highest economic impact due to their damage to crops or their role as vectors for human diseases. Although biocontrol falls outside of the scope of the present review, considerable efforts have been directed at identifying specific bacteria that could serve as biocontrol agents against insect pests (e.g. Caragata et al. (2019); Hernández et al. (2024)). Invertebrates are also simpler

organisms that pose fewer practical challenges than vertebrates in terms of sampling and experimental manipulation for microbiome studies. In addition, they usually harbour less complex microbial communities that, in some cases, have already been well characterised (e.g. *Wolbachia* spp. in insects, Kaur et al. (2021)). Conversely, some other host taxa are under-represented despite being common invaders. For instance, we found very few studies on the microbiome of invasive birds which could be related to the technical challenges of obtaining high-quality microbial data from their faecal samples compared to other vertebrate classes (Pietroni et al. 2024).

Research also varied in terms of which of the host's microbial communities was studied (Fig. 2b). Most of the research papers focussed on the gut microbiome (42.9%, n = 60), but several studies on invertebrates characterised the microbial community of the entire, homogenised specimen (21.4%, n = 30). Analysing exclusively the skin/exoskeletal microbiome (5.7%, n = 8) was done in one invertebrate study, but was especially common for introduced amphibians and fish, while a single study (0.7%) on mammals focussed exclusively on the oral microbiome. A further 11.4% (n = 16) of studies, all of them on invertebrates or amphibians, jointly analysed microbiomes from multiple tissues or organs within a single invasive animal species. Finally, while analysing some environmental samples along with host samples was common for soil or aquatic invasive organisms, there were several studies (17.9%, n = 25) that did not analyse any host organ or tissue, but focussed exclusively on the microbiome of the surrounding environment to detect any alteration related to the presence of the invasive species.

In terms of design, 39.9% (n = 56) of the research articles were descriptive, with a primary focus on characterising the composition of an invasive species' microbiome or its impact on the surrounding environment, while the remaining 60.1% (n = 84) of research papers included a comparative aspect. Earlier studies were more frequently descriptive in nature, while, from 2018 onwards, there is an increase in the number of more complex, comparative study designs that try to infer the role of the microbiome in the invasive species' adaptation (Fig. 2a).

Patterns in animal invasions and the microbiome

We used the subset of the 43 comparative research papers for a more in-depth analysis to gain further insight into whether the microbiome is a driver or facilitator of invasiveness. The articles included in the subset of comparative studies either compared the microbiome of the invasive species to a native counterpart (17 articles) or the microbiome of the invasive species across its native and introduction range (17 articles) or along the invasion wave (6 articles). Three articles compared the microbiome of the invasive species both against the competing native species and across ranges. Most of these studies still targeted invertebrate hosts (26 articles), but vertebrates were relatively well represented (14 articles). We observed that a few invasive species-microbiome systems have been explored more in depth through multiple comparative studies (listed in Table 2).

The microbiome across geographic ranges

A prominent question when addressing biological invasions and microbiomes is certainly the fate of an invasive host's microbial community after its establishment in a new range. In most cases and across a range of diverse host taxa,

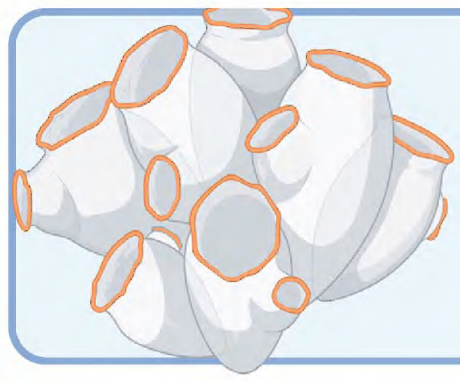
Table 2. List of the invasive animal-microbiome systems assessed by multiple comparative studies with corresponding references.

Invasive host species	References
Asian tiger mosquito (*Aedes albopictus*)	(Minard et al. 2015, Rosso et al. 2018)
Common wasp (*Vespula vulgaris*)	(Lester et al. 2015, Gruber et al. 2019)
Oriental fruit fly (*Bactrocera dorsalis*)	(Liu et al. 2016, Wang et al. 2023)
Warty comb jelly (*Mnemiopsis leidyi*)	(Jaspers et al. 2019, 2020)
Signal crayfish (*Pacifastacus leniusculus*)	(Dragičević et al. 2021, 2024, Grbin et al. 2023)
Lionfish species complex (*Pterois volitans/P. miles*)	(Stevens and Olson 2013, 2015, Stevens et al. 2016)
Red-eared slider (*Trachemys scripta elegans*)	(Qu et al. 2020, Meng et al. 2023)
Cane toad (*Rhinella marina*)	(Abarca et al. 2018, Christian et al. 2018)

microbiomes in the invaded range were found to be significantly distinct from those in the native range (Diptera: Minard et al. (2015); Martinez-Sañudo et al. (2018); Rosso et al. (2018); Hymenoptera: Gruber et al. (2019); Rothman et al. (2021); Tuerlings et al. (2023); ctenophores: Jaspers et al. (2019); ascidians: Utermann et al. (2020); Goddard-Dwyer et al. (2021); fish: Stevens and Olson (2015); Escalas et al. (2022); amphibians: Abarca et al. (2018); Wagener et al. (2022); Leonhardt et al. (2023)). Wild animals' microbiomes are generally highly variable in space and time (Neu et al. 2021; Perlman et al. 2022), but host species are expected to maintain a core of microbes which are most relevant for the host biological function and/or the stability of the community itself (Risely 2020). While there is no unique definition of what constitutes a species' core microbiome (Risely 2020; Neu et al. 2021), the maintenance of a conserved set of microbes (or functions) across native and introduction ranges was observed in several of these systems, notwithstanding the dissimilarity in microbiome structure. Some examples are detailed in Fig. 3 (Stevens and Olson 2015; Stevens et al. 2016; Abarca et al. 2018; Utermann et al. 2020).

There are, however, a few exceptions to this pattern: treehoppers *Stictocephala bisonia* (Szklarzewicz et al. 2020) and brown widow spiders *Latrodectus geometricus* (Mowery 2024) maintain a highly conserved microbiota across their native range and through multiple introduction areas. The microbial communities of these two arthropods are composed of only a handful of vertically transmitted species, strongly suggesting that these are all obligatory symbionts which are crucial for host survival. To a lesser extent, the globally invasive and polyphagous medfly (*Ceratitis capitata*) was also found to harbour very similar communities across multiple biogeographical regions, suggesting that it has attained a highly functional microbial assemblage that allows the host to feed on a wide range of plants (Arias et al. 2022).

Regarding the diversity of microbiomes across ranges, several of the comparative studies found that individuals from invasive populations had, on average, higher microbial richness (Abarca et al. 2018; Utermann et al. 2020; Arias et al. 2022; Escalas et al. 2022) or more complex microbial networks (Gruber et al. 2019) than those from native populations. However, other studies found the opposite pattern (Minard et al. 2015; Lester et al. 2017; Rosso et al. 2018; Goddard-Dwyer et al. 2021) or no difference at all (Lester et al. 2015; Martinez-Sañudo et al. 2018; Rothman et al. 2021; Wagener et al. 2022). No phylogenetic host group appears to be predominantly associated with a particular pattern and, in at least one case, contrasting diversity patterns were even



Invasive populations of the ascidian *Ciona intestinalis* in the northwest Atlantic have a distinct microbiota from those in the native European range, but all share several bacterial taxa capable of producing antimicrobial and antifouling compounds (Uterman et al. 2020).

The skin microbiome of cane toads (*Rhinella marina*) in Puerto Rico is distinct from the source population in Costa Rica, but they retain a common core of species known to enhance host resistance to chytridiomycosis and other diseases (Abarca et al. 2018).

Lionfish populations (*Pterois volans/P. miles complex*) introduced to the Caribbean have distinct skin microbiomes from those in the Indo-Pacific (Steven and Olson 2015), but share a similar core of microbes associated with antimicrobial activity against fish pathogens (Stevens et al. 2016).

Figure 3. Microbiomes across ranges. The microbiome of invasive populations is often distinct from that of populations in the native range, but they typically retain a core of microbial species involved in modulating key phenotypic traits. Created in BioRender (https://BioRender.com/a68e550).

observed by different studies on the same target species (Lester et al. (2015) and Gruber et al. (2019) on common wasps, *Vespula vulgaris*). While it would be tempting to assume that a higher compositional diversity in the microbiome directly translates into higher fitness and adaptability, this is not necessarily the case (Reese and Dunn 2018; Williams et al. 2024). Instead, functional information remains crucial to disclose the relationship between microbiome diversity and host phenotypic traits.

The microbiome across competing species

Some further insight into diversity patterns and invasions comes from those studies that compared the microbiota of an invasive species to that of some ecologically similar, co-occurring native species. In many cases, such studies found that the invader harboured a microbial community that was taxonomically and functionally more diverse compared to the native species (Stevens and Olson (2013) on fish, Duguma et al. (2017) on mosquitoes, Chiarello et al. (2022) on bivalves, Do et al. (2023) on hymenoptera, Hall et al. (2024) on squirrels). However, some other studies found a slightly different pattern, with invaders having a microbiota that was less diverse, but still enriched in some relevant functional traits (Santos et al. (2021) on amphibians, Zuo et al. (2024) on bivalves), showing how diversity metrics alone sometimes might fail to tell the whole story. For instance, Zuo et al. (2024) found that the microbiome of recently established charru mussels (*Mytella strigata*) in China was less diverse than that of native, outcompeted, *Perna viridis* inhabiting the same reef.

Nevertheless, the relative abundance of taxa, metabolites and enzymes related to carbohydrate degradation was significantly higher in *M. strigata*, suggesting that the invader might be more efficient at energy uptake despite harbouring a lower diversity of microbes. Some additional examples of invasive species having a higher microbiome's functional potential than their native competitors are detailed in Fig. 4 and include traits potentially related to a broader diet range (Chiarello et al. 2022; Hall et al. 2024) or to a higher tolerance to anthropogenic stressors (Santos et al. 2021).

Regardless of diversity patterns and similar to what emerged from across-range comparisons, in most cases, the microbiome of the invasive species was clearly distinct from that of co-occurring native species, even when they were phylogenetically very close and/or ecologically very similar (Stevens and Olson 2013; Duguma et al. 2017; Christian et al. 2018; Wilches et al. 2018; Jaspers et al. 2020; Santos et al. 2021; Zhu et al. 2022; Tuerlings et al. 2023; Vasconcelos et al. 2023; Hall et al. 2024). This is hardly surprising, as subtle physiological or anatomical differences between host species can result in relevant differences at the microscale and lead to very distinct microbial assemblages (Maritan et al. 2024), even in species that share the same environment and have largely overlapping niches. Still, a few studies reported some extensive level of homogenisation in the microbiota of invasive and co-occurring native species. This was the case for the exoskeletal microbiota of invasive signal crayfish (*Pacifastacus leniusculus*) and native narrow-clawed crayfish (*Pontastacus leptodactylus*) inhabiting the same river area in Croatia (Grbin et al. 2023), as well as for the gut microbiota of invasive Asian hornet (*Vespa velutina*) and four native, co-occurring *Vespa* spp. in South Korea (Do et al. 2023). Even in these cases, though, some relevant species-specific patterns were identified in the form of differentially abundant taxa.

Although the microbiome composition of invasive Asian clams *Corbicula fluminea* in the southeastern USA indicates some horizontal transfer with co-occurring native bivalves, the species has higher richness and functional potential, enriched in degradation pathways (Chiarello et al. 2022).

The skin microbiota of Asian common toads (*Duttaphrynus melanostictus*) introduced to Madagascar has a higher xenobiotic degradation potential compared to native ridged frogs (*Ptychadena mascareniensis*), possibly leading to a higher tolerance to anthropogenic stressors (Santos et al. 2021).

The gut microbiome of invasive grey squirrels (*Sciurus carolinensis*) in the UK is more diverse than that of native red squirrels (*S. vulgaris*), and enriched in bacterial taxa associated with the fermentation of plant-based materials, which may explain their wider diet range (Hall et al. 2024).

Figure 4. Microbiomes across species. The microbiome of invasive species often has a higher functional potential than that of co-occurring, outcompeted native species. Created in BioRender (https://BioRender.com/v46k439).

Drivers of microbiome assembly during invasions

The microbiome is an assemblage of species acquired by the host through a combination of vertical transfer from its parents and horizontal transfer from other co-occurring organisms and the environment (Maritan et al. 2024). As described in the previous sections, both processes are observed and variably predominant in invasions. At one end of the spectrum, we have invasive species that maintain a completely conserved, vertically transmitted microbiota across ranges (Szklarzewicz et al. 2020; Mowery 2024) and, at the other end, species showing a strongly environmentally-driven assembly resulting in microbial communities that largely overlap with those of co-occurring native species (Do et al. 2023; Grbin et al. 2023). However, in an invasion context, stochastic events related to the invasion process will play a large part in driving the assembly of the "new" microbiome. This would be similar to what often occurs to pathogen communities of invasive species, with rare species lost via founder effects or population bottlenecks and others acquired from the local environment after introduction (Torchin et al. 2003; MacLeod et al. 2010).

Studies that analysed variation in the structure and composition of microbiomes along the invasion path of a species can offer further insight into microbiome dynamics during invasions. For instance, Argentine ants (*Linepithema humile*) were introduced through serial jumps from Argentina to the USA, to Australia and finally to New Zealand and their microbial communities show a progressive decrease in richness and in the relative abundance of core taxa along this path, mirroring a series of bottlenecks in the host population (Lester et al. 2017). Propagule pressure (i.e. a combined measure of the frequency of introductions and the number of individuals per introduction, Lockwood et al. (2005)) is another factor that can potentially affect microbial assemblages in invasive species. Rosso et al. (2018) found that Italian populations of the Asian tiger mosquito (*A. albopictus*) have a depauperate microbial community compared to French populations (Minard et al. 2015) and suggest that this might be the result of fewer introduction events occurring in Italy. Population mixing between invaders of different origin (Wang et al. 2023, see next section) or even hybridisation between different invasive species (Zhu et al. 2021) can further contribute to microbiome differentiation. Asian bigheaded carps (*Hypophthalmichthys nobilis*) and silver carps (*H. molitrix*) introduced into the Mississippi River Basin (USA) were found to extensively hybridise (Lamer et al. 2015). The gut microbiome of hybrids shows several features that are intermediate to those of the parental species, but has also a tendency for higher diversity and presents some unique traits such as a higher relative abundance of taxa involved in ammonium oxidation and an elevated proportion of putative genes related to the digestion of phytoplankton (Zhu et al. 2021).

Decoupling stochastic processes from adaptive shifts in the microbiota can be challenging. Escalas et al. (2022) characterised the gut microbiome of tropical rabbitfish *Siganus rivulatus* and *S. luridus* along their invasion path from the Red Sea to the central Mediterranean and found strong modifications in its structure and composition with increasing distance from the native range. In parallel with a general increase in richness and entropy at the individual level, they also observed a progressive homogenisation of the microbial community both among individuals and between the two species. A reduced variability in community structure within invasive populations can be an indication of stochastic events when coupled to a reduced genetic diversity in the host population, such as in the ascidian

Clavelina oblonga (Goddard-Dwyer et al. 2021). In the case of rabbitfish, however, the genetic structure of Mediterranean populations is similar to Red Sea ones, with no sign of bottlenecks (Hassan et al. 2003; Azzurro et al. 2022). In addition, the rabbitfish microbiota at each site is also distinct from that of the surrounding water and invasive populations have a distinct functional potential related to short chain fatty acids metabolism (Escalas et al. 2022). The observed shift in microbial communities appears then as the result of rabbitfish adapting to a new and more diverse diet in the Mediterranean, where brown macroalgae abundant in the Red Sea are scarce and was likely a key feature for their adaptation to the new range.

As seen with other, non-invasive species (Moeller et al. 2017; Härer and Rennison 2023), a common pattern that emerges from studies comparing different host populations along the invasion wave is that microbiome dissimilarity tends to increase with increasing geographic distance from the source population (Lester et al. 2015, 2017; Jaspers et al. 2019; Escalas et al. 2022; Wagener et al. 2022; Leonhardt et al. 2023). Such differentiation can be extremely rapid: overall the gut microbiome of guttural toads (*Sclerophrys gutturalis*) introduced in Cape Town (South Africa) 20 years ago has diverged compositionally from their source population, but extensive divergence was also found between core and front populations within the introduction area itself, suggesting rapid alteration during range expansion (Wagener et al. 2022). Similarly, along the expansion range of the the oriental fruit fly (*Bactrocera dorsalis*) in China, the microbiome of early-established populations (dating back to the 1970s) is clearly distinct and more diverse than that of late-established ones (2000s) (Liu et al. 2016).

Finally, it must be considered that several vertebrate invasions result from accidental or intentional release from captivity and captivity is another factor that can strongly alter microbial assemblages (McKenzie et al. 2017; Alberdi et al. 2021; Dallas and Warne 2023). As an example, when comparing the gut microbiome of free-ranging and captive American minks (*Mustela vision*) and European minks (*M. lutreola*) in Spain, van Leeuwen et al. (2023) found that captivity led to depauperate communities and its effect even surpassed differences between host species. This reduction in richness was particularly strong in invasive individuals that experienced poorer welfare and management conditions while in captivity (i.e. fur farming vs. captive breeding programme for repopulation).

The microbiome as a driver of invasiveness

Although most of the research included in the present review is observational, some recent studies explored the mechanistic link between microbiome composition and invasiveness traits through experimental set-ups.

Fontaine and Kohl (2020) compared the response of tadpoles' gut microbiota to a temperature gradient in two ecologically similar North American frog species: the globally invasive bullfrog (*Lithobates catesbeianus*) and the congeneric green frog (*L. calmitans*), which is instead restricted to its native range. As predicted, the invasive species showed a highly plastic microbiota that responds more rapidly to temperature changes, both compositionally and functionally, which might contribute to its great invasion success. Specifically, many microbial pathways were altered in bullfrogs in response to treatment and about a third of these were enriched at warmer temperatures, suggesting an adaptive change in microbial metabolism. Conversely, microbial metabolism in green

frogs showed fewer and slower changes, and the altered pathways all had a decreasing trend, suggesting metabolic depression.

In a similar experiment, Meng et al. (2023) analysed the response of three freshwater turtles in China (native *Mauremys reevesii*, alien - but not invasive - *Pseudemys nelsoni* and invasive *Trachemys scripta elegans*) to varying concentrations of ammonia in terms of swimming performance, gut microbiota composition and liver metabolomic profiles. In this case, however, only the latter were significantly altered in response to treatment and, in particular, amino acids and energy metabolites were strongly reduced in *M. reevesii* and *P. nelsoni*, but not in *T. s. elegans*, suggesting that the invasive species may be more resistant to pollution. Conversely, the diversity and structure of gut microbial communities were unaffected by ammonia exposure in all species and, although the authors report that the relative abundance of some microbial genera varied with ammonia concentration, the lack of functional information on microbial metabolism does not allow much inference on the possible adaptive significance of such changes.

Another experiment addressing the role of microbiomes in invasions concerns the fall webworm (*Hyphantria cunea*), a globally invasive North American moth. During the last decades, the species has spread throughout China's temperate regions and it is now expanding further south, into subtropical areas. Zhang et al. (2024) characterised the gut microbiome of *H. cunea* larvae across these regions, to explore its influence on survival and adaptation to such a broad range of habitats and host plants. Larvae sampled on different plants showed highly dissimilar microbiomes and, in particular, larvae from southern populations sampled on toxic *Metasequoia glyptostroboides* had the most diverse and distinct microbial community, enriched in taxa associated with detoxification. The authors further showed that larvae from northern populations fed with *M. glyptostroboides* have higher mortality compared to southern ones that are adapting to this new host plant. A final microbiota transplantation experiment from southern larvae into northern larvae boosted the survival rate of the latter on *M. glyptostroboides*, confirming that the microbiome is playing a key role in the rapid adaptation of this invasive species to new habitats and food sources.

As mentioned before, repeated introductions followed by population mixing could promote increased diversity of microbial communities and prove beneficial for host fitness. Populations of the invasive oriental fruit fly (*B. dorsalis*) in northern China appear to be hybrids of lineages originating from different biogeographical regions following multiple introductions (Aketarawong et al. 2007; Qin et al. 2018). In a recent study, Wang et al. (2023) compared the fitness and microbiome of lab-reared lines of *B. dorsalis* originating from outbred, invasive populations with those of lines originating from inbred populations. They found that outbred flies had higher heterozygosity and fitness (i.e. survival rate, pupal weight and egg output), as well as a compositionally and functionally richer microbiome and higher concentrations of several amino acids. Supplementing inbred individuals with some of these amino acids and feeding them with the spent diet from outbred flies both resulted in a significant increase in their fitness. The authors further characterised the intestinal transcriptome of the two phenotypes, showing that several pathways related to immunity and growth are upregulated in outbred individuals. This led them to conclude that compositional changes in the microbiome determine an increase in the concentration of specific amino acids which leads, in turn, to transcriptional shifts promoting growth, development and ultimately invasiveness.

Knowledge gaps, best practices and research priorities

Our review of the existing literature shows that most of the published studies are still descriptive, that technical and analytical methods are far from standardised and that some host taxa are still poorly represented, hindering the possibility of conducting robust quantitative meta-analyses. However, publication trends suggest that interest in the topic is steadily growing and we are confident that more data will soon become available, allowing for meta-analytical approaches that will enable researchers to address broader eco-evolutionary questions regarding the role of animal-associated microbiomes in invasions.

For instance, contrasting diversity patterns emerged from both across ranges and across species comparisons, but the number of studies is still too limited to identify any consistent associations with, for example, host phylogeny. Another interesting question to address would be whether it is more advantageous for an invading species to have a more plastic or conversely a more resistant microbial community. From a slightly different perspective, one could also ask whether some bacterial taxa — or functions — might be more beneficial to conserve — or acquire — than others. It is likely that the answers to such questions would be highly dependent on the host species, the invasion context and the specific functional role of the different microbial taxa, but as more data become available, meta-analyses could potentially reveal broader underlying patterns related to the characteristics of the invaded habitats or the phylogeny and/or niche specialisation of the host or microbial taxa.

Further system-specific research is, therefore, needed to enable researchers to address these broader questions, but it is important that future studies adhere to some common standards in order to be comparable and have inferential value. For instance, our review highlights that the vast majority of comparative studies are still observational in nature, echoing the findings of a recent systematic review on microbe-driven adaptation in wild vertebrates (Martin Bideguren et al. 2024). While we acknowledge that conducting experimental studies in wild animals, especially vertebrates and on a large scale can be challenging, experimental evidence is needed to elucidate the mechanistic link between microbiome composition and host adaptation (Kohl 2017; Davidson et al. 2020; Koh and Bäckhed 2020). In particular, experimental manipulation of hosts' microbiota through faecal transplants or antimicrobial administration is a robust way to test causality in microbiome-related hypotheses (Koh and Bäckhed 2020). For example, thanks to a microbial transplant, Zhang et al. (2024) were able to demonstrate that the adaptation of the invasive fall webworm (*H. cunea*) to new host plants is microbiome-mediated.

Nevertheless, we argue that, at this early stage, comparative, observational studies are still valuable to shed light on whether animal microbiomes may be relevant drivers of invasiveness in any way. In such a high-dimensional and complex system as the host and its microbiome, correlative studies can help to sort out potentially influential patterns that can later be addressed by an experimental approach to prove causality and determine its direction (Davidson et al. 2020). Our review shows, for instance, that comparisons across geographic ranges can reveal changes in microbiome composition and/or functionality potentially linked to the adaptation to the new range and to a successful invasion. Similarly, comparisons between different populations along the invasion path can shed light into processes affecting the assembly of microbial communities. Lastly, comparing the microbiome of invasive species against that of outcompeted, phylogenetically close native species

can offer some insight into whether differences in microbiome functionality play a part in their competitive interaction.

However, two requirements are essential for such correlative studies to be meaningful and have some inferential value: first, the use of an appropriate sampling design and second, the generation of robust functional information alongside taxonomic data. Wild animals' microbiomes usually show high intra- and inter-individual variation; hence, working at the appropriate spatial and temporal scales, sampling multiple populations, as well as choosing the right microbial taxonomic resolution are fundamental to avoid sampling artefacts (Knight et al. 2018; Neu et al. 2021; Zoelzer et al. 2021; Degregori et al. 2024). For instance, Tuerlings et al. (2023) found that the microbiome of common wasps (*V. vulgaris*) in the introduction range was completely distinct from the one in the native range, but they point out that this result might be an artefact linked to the limited number of populations sampled in the latter. Similarly, Qu et al. (2020) found that native (*Chinemys reevesii*) and invasive (*T. scripta elegans*) freshwater turtles had similar gut microbiota, but they acknowledge that their small sample size might have failed to capture the full extent of the microbiome composition in the two species.

In terms of functional inference, we advocate for a more widespread use of shotgun metagenomics, since reliable and complete functional information is critical for drawing conclusions about observed microbiome shifts or differentially abundant microbial taxa (Quince et al. 2017; Pérez-Cobas et al. 2020). Whenever cost is a relevant constraint, a possible solution would be to use a mixed approach (e.g. Jang et al. (2022); Zhang et al. (2023, 2024)), applying amplicon sequencing to the entire sample set and shotgun to a representative subset, to derive functional information while limiting sequencing costs. However, the application of different analysis methods should be carried out considering the biological and technical factors that can easily lead to biased or inconclusive results (Aizpurua et al. 2023; Pietroni et al. 2024). Large-scale standardisation initiatives like the Earth Hologenome Initiative (Leonard et al. 2025) can be instrumental in achieving that goal. The ultimate aim should be to couple microbiome compositional and functional information with measures of host fitness (e.g. Wang et al. (2023); Zhang et al. (2024)) and/or other -omics approaches, such as metabolomics (e.g. Utermann et al. (2020); Zuo et al. (2024)) or transcriptomics (e.g. Wang et al. (2023)), to both establish causal relationships and gain insight into the mechanistic processes linking microbiome dynamics with animal invasiveness.

Conclusions

Our review of the existing literature shows that the attention of the scientific community to the role of the microbiome as a potential driver of animal invasions has steadily increased over time, but research is still taxonomically biased and mostly observational in nature. The analysis of the subset of comparative studies shows that, in most systems, the host microbiome undergoes relevant changes during the introduction process and many of these shifts appear to have some adaptive value. Several studies also highlight the importance of stochastic processes in determining the post-invasion microbial community. However, to date, only a handful of experimental studies have demonstrated the mechanistic link between the microbiota and invasiveness in an animal species. More such studies are needed to elucidate whether adaptive shifts in microbial communities following invasion are a common occurrence. We believe that observational studies remain valuable, but only when combined with a robust

sampling design and strengthened by measures of host fitness and the adoption of new analytical approaches that allow for more robust functional inference. As more complete, system-specific studies become available, meta-analytic approaches will allow researchers to compare the dynamics of microbial communities across multiple invasive species and ecosystems and, potentially, uncover broader eco-evolutionary patterns related to the role of microbiomes in animal invasions.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

No new data were analysed or generated for this study. The full list of articles included in the review is provided as Suppl. material 2.

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Supplementary material 1

PRISMA flowchart

Authors: Claudia Romeo, Elsa Brenner, Lucas A. Wauters, Antton Alberdi

Data type: pdf

Explanation note: PRISMA flowchart illustrating the systematic review process.

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Supplementary material 2

List of reviewed articles

Authors: Claudia Romeo, Elsa Brenner, Lucas A. Wauters, Antton Alberdi

Data type: csv

Explanation note: Full list of the 147 articles included in the review, their metadata and associated descriptors.

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Supplementary material 3

Study design descriptors

Authors: Claudia Romeo, Elsa Brenner, Lucas A. Wauters, Antton Alberdi

Data type: pdf

Explanation note: Description of the categories used to define the study design of the assessed articles.

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